

A NEW SPECIES OF LIZARD (*TILIQUA*)
FROM THE MIOCENE OF RIVERSLEIGH, QUEENSLAND

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A new species of *Tiliqua*, *T. pusilla*, is described from fossil dentaries from the Gag locality, Dwornamor local fauna, Middle Miocene of Riversleigh, Queensland. The new species is characterised by its distinctive rounded cheek teeth and very small size. □ *Tiliqua*, Scincidae, dentition, Miocene, Riversleigh.

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The limestone deposits of the Riversleigh area of northwestern Queensland (recently reviewed by Archer et al., 1989) are becoming widely known as a source of excellently preserved vertebrate fossils, ranging in age from the late Oligocene to the Pleistocene. The limestone matrix has enabled acid preparation of delicate bones (e.g. bat skulls) in perfect condition and many thousands of specimens have already been recovered. The detailed preservation and the evident terrestrial nature of some of the faunas are factors suggesting that small reptiles such as lizards, which normally fossilise poorly, would be preserved, and such is the case. Members of the families Agamidae, Varanidae, Gekkonidae and Scincidae have been identified in the collections from Riversleigh. An initial survey of the agamids has just been completed (Covacevich et al., 1990) and we report here on one of the scincid lizards. The Scincidae is the most diverse family in the modern Australian fauna. It includes many highly characteristic forms, suggesting a long period of evolution in Australia about which almost nothing is known. The Riversleigh deposits are the first from the Australian Tertiary known to be rich in fossil skinks (Hutchinson, 1992).

To date, most of the remains identified as lizards are partial or fragmentary lower jaws. These are difficult to identify because there are too few data concerning taxonomic variation in skeletal characters of the very diverse modern Australopapuan fauna. However, one of the most distinctive Australian genera, *Tiliqua* (s.l.), has long been recognised as having unusual teeth (e.g. Smith, 1937), with several of the posterior cheek teeth markedly enlarged and having conical or rounded crowns. Shea (1990) described the *Tiliqua* lineage: a revised *Tiliqua* (including

Trachydosaurus), plus *Cyclodomorphus*, the latter including the slender species *gerrardii*, *casuarinae* and the *branchialis* complex. Both genera have characteristic dental morphology which allows isolated dental arcades to be identified to species (Archer and Brayshaw, 1978; Bartholomai, 1977; Shea, pers. obs.).

Amongst the material from Riversleigh are two partial dentaries with the enlarged, round-crowned teeth of the *Tiliqua* lineage. These specimens are here described as a new species of *Tiliqua*, the first extinct member of the genus to be described.

MATERIALS AND METHODS

Prepared fossil specimens of lizard jaws were provided by Dr M. Archer, University of N.S.W. These had been sorted from concentrate obtained by the acid processing of limestone blocks from Riversleigh Station, northwest Queensland. Reference material of modern taxa was obtained from the following collections: American Museum of Natural History, New York; Australian Museum, Sydney; Queensland Museum, Brisbane (QM); Queen Victoria Museum, Launceston; South Australian Museum, Adelaide (SAMA); Western Australian Museum, Perth; Zoologisches Museum, Humboldt Universität, Berlin. Specimens were examined, measured and drawn using a Wild M3Z stereomicroscope with an eyepiece micrometer and drawing tube.

SYSTEMATICS

Family SCINCIDAE

Subfamily LYGOSOMINAE Mittleman, 1952

Tiliqua Gray, 1825

Tiliqua pusilla sp. nov.
(Figs 1-2)

MATERIAL EXAMINED

HOLOTYPE: QM F16876 (formerly M. Archer collection no. AR5337a).

PARATYPE: QM F16877 (formerly M. Archer collection no. AR4183).

TYPE LOCALITY: Gag locality, one of the lowest of the Tertiary System C group (of sites on the Gag Plateau, Riversleigh Station, Queensland (precise details of site available from University of NSW Vertebrate Palaeontology Laboratory). Matrix of freshwater limestone. The Gag site has yielded the Dwormamor local fauna and is of probably early Middle Miocene age (c. 15 Myr BP; Archer et al., 1989).

DIAGNOSIS

A small species (estimated dentary tooth row length of the holotype, 9mm), cheek teeth enlarged, with crowns blunt and slightly rounded in lingual profile, more conical in mesial profile, apices bearing a shallow central pit from which radiate striae.

DESCRIPTION

HOLOTYPE: (Fig. 1 a-b) A partial left dentary, missing its rostral third and the caudal, non-tooth bearing extremity, including all of the coronoid process and the apex and ventral margin of the angular process. Meckelian groove closed, no trace of suture. Rostral end of ventral margin with a low ridge, presumably the caudoventral extremity of the symphyseal crest. Apex of splenial notch (rostral margin of inferior alveolar foramen) lies at midpoint of interval between coronoid border of dorsal medial lamina and caudal margin of symphyseal crest. Coronoid margin of dorsal medial lamina obtusely angulate. Lateral surface with a deep, well-defined arcuate muscle scar caudal to level of last tooth, presumably for the *M. adductor mandibulae externus superficialis* (AMES) (part IV, Wineski and Gans, 1984).

Internal septum fused ventrally along entire length to ventral medial lamina, completely separating inferior alveolar canal from Meckelian canal. Caudal margin of internal septum with two notches (caudodorsal and rostroventral) for articulation with surangular.

Labial wall of dental sulcus tall and robust, lingual wall almost absent, but lingual margin well-defined and sharply angulate. Dentition pleurodont. Seven closely-packed teeth of even occlusal height and two unfilled tooth loci present, in order from mesial to distal: a tooth locus for a

similar-sized tooth to those immediately caudal, at the level of the caudal extent to the ventral symphyseal crest; a tooth, missing crown, with a small resorption pit at base; an intact, unresorbed tooth; a tooth largely resorbed at the base, but with intact crown; a tooth with a small resorption pit basally, but with mesial margin of crown missing; a very large empty tooth locus for a tooth approximately twice the diameter of the preceding teeth; a large tooth (only slightly less in diameter than the preceding locus) with intact crown, but with a large resorption pit basally; two intact teeth, the second with a small resorption pit, both abruptly narrower and shorter (occlusal surface lower) than the preceding tooth. Tooth crowns bluntly rounded in lingual profile, slightly more conical in mesial profile, the largest extant tooth even more flattened; mesial teeth with a shallow apical notch, from which striae radiate towards the periphery of the crown; similar, shallower striae present on more caudal teeth.

PARATYPE: (Fig. 1 c-d) The entire rostral half of a left dentary, broken at the level of the 11th tooth and apex of splenial notch, but with most teeth either broken or missing. The portion overlapping with the holotype (tooth loci 5-11) is similar to it in all respects, but slightly smaller. In dorsal view, dentary nearly straight. Symphysis flattened, angle between symphyseal surface and lingual surface obtuse, slightly rounded. Angle between mandibles (as estimated by apposition of a mirror image) 41° internally, 50° externally.

Lateral surface with six irregularly spaced mental foramina. Teeth and loci are present as follows, from mesial to distal: Five teeth, obliquely fractured at base to leave only the implanted portion, the fifth level with the end of the ventral symphyseal crest; a tooth missing lateral surface of crown; an empty tooth locus of similar size to the preceding teeth; a tooth broken transversely at level of margin of mandible, missing entire crown; an entire, unworn tooth with a fracture line below the crown; a very large empty tooth locus for a tooth approximately twice the diameter of the preceding teeth, and a large tooth stump, similar in diameter to the preceding empty tooth locus, missing crown. Resorption pits are present in the bases of the second, fifth, eighth and eleventh teeth. The single intact tooth (ninth) slanting labially about 30° from vertical. In mesial profile, lingual wall nearly straight, labial wall of crown slightly bulbous, apex moderately narrow, conical, but with a prominent mesiodistal apical notch. In lingual view, crown more rounded, slightly

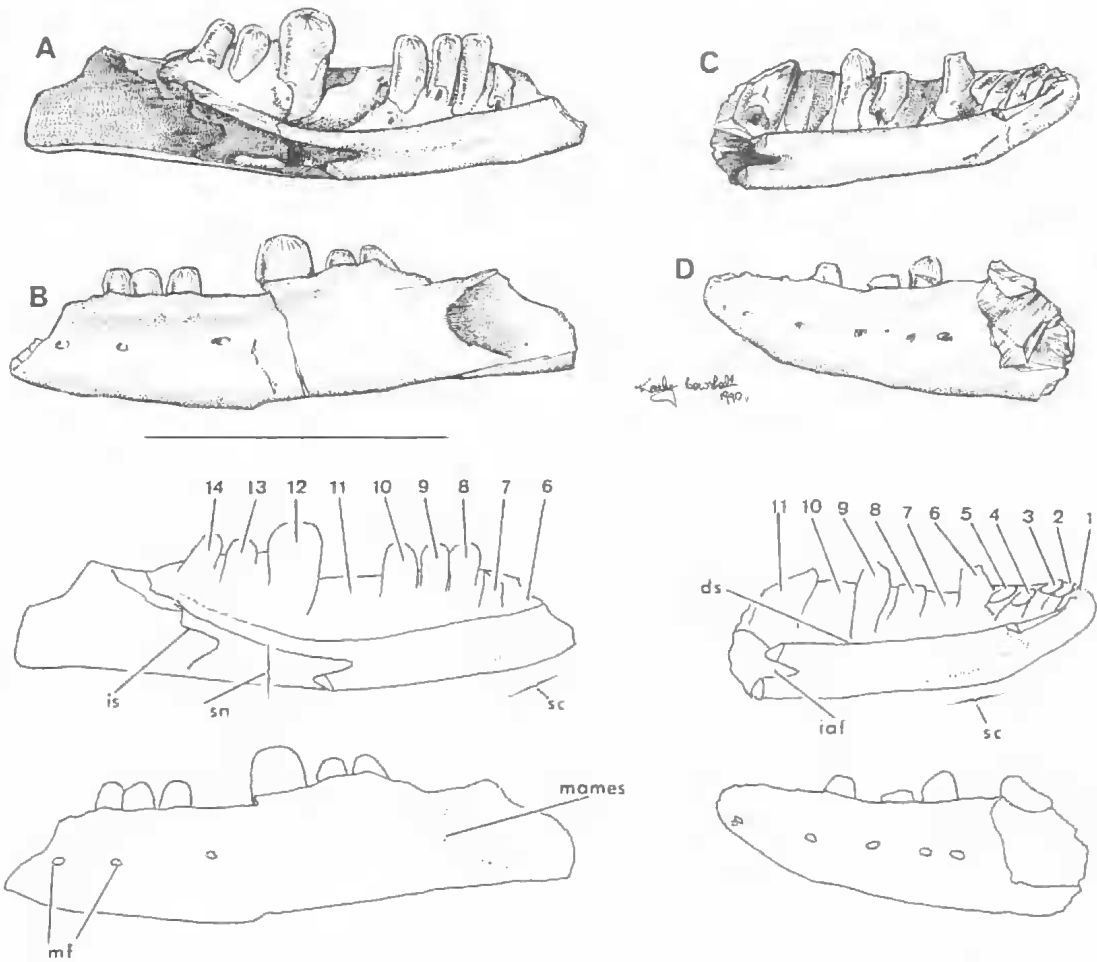


FIG. 1. *Tiliqua pusilla* sp. nov. Holotype (QM F16876, A-B) and paratype (QM F16877, C-D) partial left dentaries in lingual (A, C) and labial (B, D) views. Scale bar equals 5mm. Abbreviations: ds, dental sulcus; iaf, inferior alveolar foramen; is, internal septum; mames, scar for mandibular adductor musculature; mf, mental foramina; sc, symphyseal crest; sn, splenial notch; numbers indicate tooth positions.

higher distally. Crown with radiating striae in occlusal view.

ETYMOLOGY

From *pusilla*, Latin adjective meaning very small.

COMPARISON WITH OTHER TAXA

The closed Meckelian groove of *T. pusilla* is a synapomorphy of both the *Egernia* and *Eugongylus* groups within the subfamily Lygosominae (Greer, 1979). Within these two groups, presence of enlarged teeth in the caudal part of the dental arcade, with the tenth or subsequent dentary tooth

largest, is a synapomorphy of the *Tiliqua* lineage (Shea, 1990).

Both specimens are nearly identical in size and morphology and presumably come from different individuals of the same species. The difference in shape of the tooth crowns in mesial profile is probably due to wear in the holotype. The paratype is complete enough to determine that the tenth and (especially) the eleventh teeth are enlarged and, by matching the positions of the symphyseal crest and inferior alveolar foramen, it is possible to overlay the two specimens to show that the large tooth preserved in the holotype is the twelfth. Figure 2 shows a composite restoration of the mandible.

Tiliqua pusilla differs from all but one of the

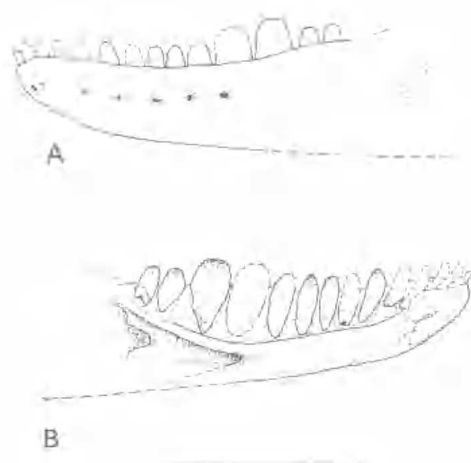


FIG. 2. *Tiliqua pusilla* sp. nov. Diagrammatic restoration of left dentary (A, labial view. B, lingual view) based on holotype and paratype specimens. Scale bar 5mm.

modern species of *Tiliqua* in its lesser size and also in tooth shape. With an estimated dentary tooth row length of 9mm, the holotype is smaller than even neonates of all *Tiliqua* except *T. adalaidensis* (neonate dentary tooth row length of other *Tiliqua* >10mm; neonate dentary tooth row length of *T. adalaidensis* not known, but adult dentary tooth row length of *T. adalaidensis* (8.2-9.3mm, n = 3). Based on the proportions of living members of the *Tiliqua* lineage, this tooth row length indicates a midline skull length of no more than 20mm. Of the seven other species of *Tiliqua*, *T. nigrolutea*, *T. occipitalis* and *T. rugosa* (Fig. 3 a-c) have conical tooth crowns in both lingual and mesial profiles, with a cutting edge directed obliquely across the crown. *T. multifasciata* (Fig. 3d), while having lower, broader teeth, also has a conical apex to the crown, but with a pronounced apical notch. *Tiliqua adalaidensis* (Fig. 3e), while more similar in size to *T. pusilla* has teeth with parallel sides, capped by a low, angulate crown in lingual profile, and slightly compressed in mesiodistal view. *Tiliqua scincoides* and *T. gigas* (Fig. 3f-g) have rounded crowns to the largest teeth and slightly more conical crowns to the more mesial teeth, but in both species a low crest obliquely crosses the occlusal surface. In *T. pusilla*, a distinct notch is present, both on the single unworn tooth of the paratype, and the slightly more worn teeth of the holotype.

Tiliqua pusilla also differs in dental morphology from *Cyclodomorphus*. The teeth of the *C. branchialis* complex (Fig. 3h-i) and *C. casuarinae*

(Fig. 3j) have more acutely conical crowns, with the apex towards the distal margin in lingual profile, or even slightly distally recurved. The other two *Cyclodomorphus* species, *C. gerrardii* (Fig. 3k) and *C. maximus*, have very rounded crowns to the largest teeth. In *C. gerrardii*, the teeth are more widely spaced, and the single enlarged tooth is both grossly larger than adjacent teeth, and much lower than in *T. pusilla*. In *C. maximus*, the teeth lack the apical notch and are relatively narrower relative to their height. Further, the mandible of *C. maximus* is relatively more gracile, which is reflected by the much narrower splenial notch in the caudal part of the dentary, and the dentary is larger overall.

Our placement of the species in *Tiliqua* rather than *Cyclodomorphus* is based on one synapomorphy and one character of uncertain polarity. *Tiliqua pusilla*, like modern *Tiliqua*, has a long, low, ventral symphyseal crest, extending caudally to the level of the fifth tooth. *Cyclodomorphus* and the closest outgroup to the *Tiliqua* lineage, *Egernia* (Shea, 1990), have a much shorter crest, which may project medially giving a hooked outline. Secondly, the angulate nature of the coronoid margin of the dorsal medial lamina is similar to that seen in modern *Tiliqua*, where it is due to enhancement of a medial buttress on the rostral process of the coronoid. In most *Cyclodomorphus* and *Egernia* the buttress is less developed and more oblique, leaving a more evenly sloping coronoid margin to the dentary.

Tiliqua pusilla is unusual compared with living *Tiliqua* in two features: its small size and the low number of dentary teeth. Both small adult size and reduced number of dentary teeth are common in *Cyclodomorphus*. Thus an explanation for the similarity between *T. pusilla* and *Cyclodomorphus* is needed. The first possibility is that the similarity in size and reduced tooth number is because the specimens of *T. pusilla* are juveniles. However, the specimens are clearly not juvenile as they have a well-defined dental sulcus with a sharply angulate lingual margin, two large teeth and the more mesial teeth subequal in size and showing several cycles of tooth replacement. In juveniles of all *Tiliqua* and *Cyclodomorphus* species, the dental sulcus is poorly-defined, its lingual margin blending with the adjacent dorsal medial lamina. There is only a single large tooth, and the teeth mesial to this one show a distinct alternation in size (Shea, MS).

Since both specimens are adult, the number of dentary teeth is lower than for adults of other *Tiliqua* species, which have more than 14 dentary

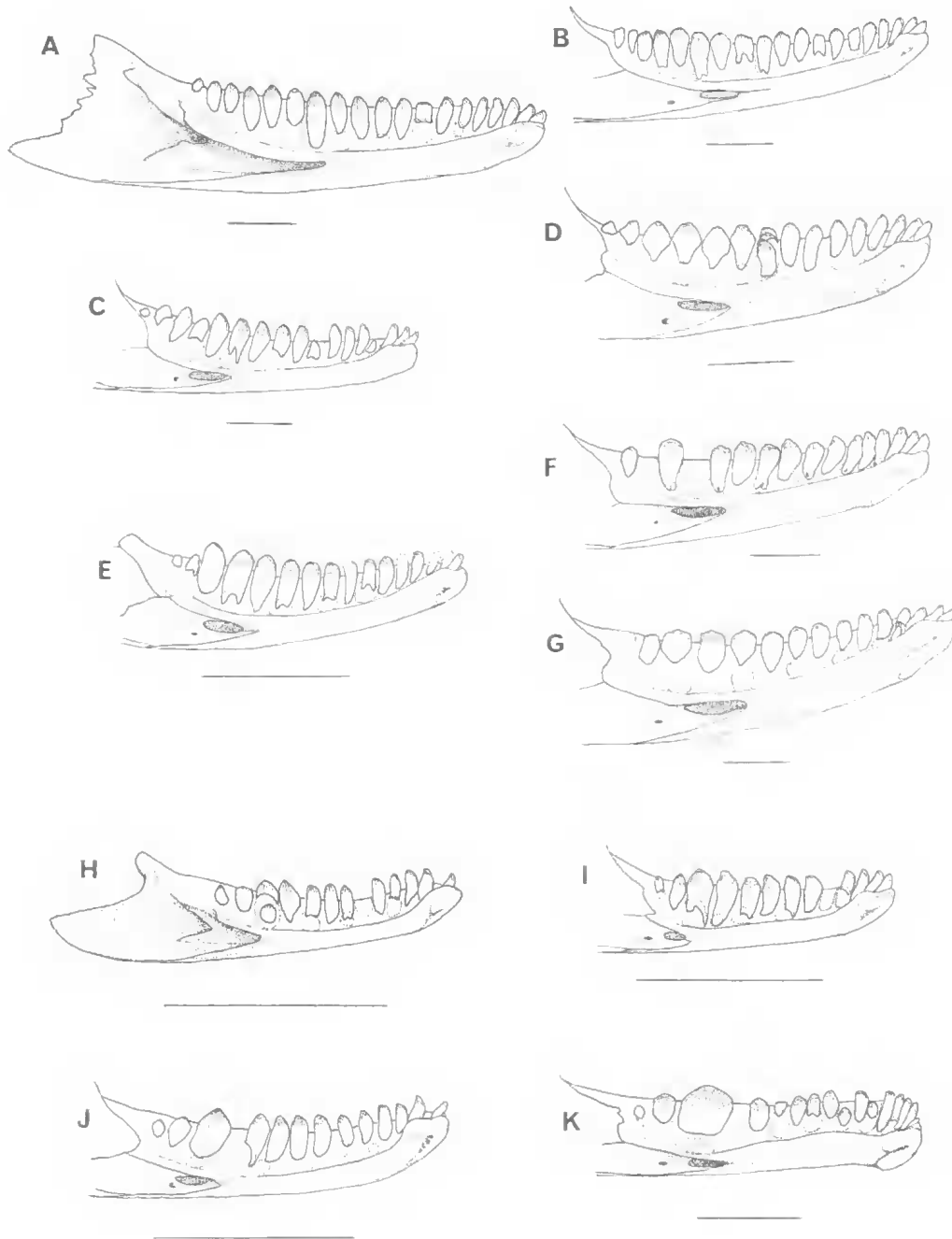


FIG. 3. Lingual views of dentaries of living species of the *Tiliqua* lineage showing variation in proportions, tooth number and shape. A and H are isolated dentaries showing the internal structure and E lacks the coronoid; the remainder are intact mandibles. A, *T. rugosa* (SAMA R27584). B, *T. occipitalis* (SAMA R35758). C, *T. nigrolutea* (SAMA R2725). D, *T. multifasciata* (SAMA R35757). E, *T. adelaidensis* (SAMA R8589). F, *T. scincoides* (SAMA R27037). G, *T. gigas* (SAMA R11419). H, *Cyclodomorphus* cf. *branchialis* (SAMA R38021). I, *C. melanops* (SAMA R37565). J, *C. casuarinae* (SAMA R35682). K, *C. gerrardii* (SAMA R35761). Scale bars 5mm.

teeth, and show a progressive distal shift in the number of the largest tooth with age, as estimated by increasing size (Shea, MS). In the *Tiliqua* lineage the two attributes (small size, reduced tooth count) are probably linked since in order to have teeth of sufficient absolute size, small species of the *Tiliqua* lineage may have to make do with fewer teeth overall in each dental arcade. Compared with the similarly-sized *T. adelaidensis*, *T. pusilla* has larger but fewer teeth (14, 11-12 largest, versus 16, 12-14 largest) and a more heavily-built jaw, and was evidently more strictly adapted for durophagy than *T. adelaidensis*, which has thinner, sharper-crowned teeth. This comparison supports the idea that the low number of teeth in *T. pusilla* is a consequence of allometric scaling, with a limit to reduction in tooth size of crushing teeth imposed by the necessity of preserving tooth strength.

DISCUSSION

Tiliqua is one of the most characteristically Australian scincid genera. Morphologically (Greer, 1970, 1979; Shea, 1990), biochemically (Hutchinson, 1981; Baverstock and Donnellan, 1990) and karyologically (Donnellan, 1985), the only living relatives of *Tiliqua* are *Cyclodomorphus*, *Egernia* and *Corucia*, collectively comprising the *Egernia* group (Greer, 1979). Little is known of the history of *Tiliqua* (or of any other skink genus) in Australia.

Tiliqua has been recorded numerous times from Pleistocene to Recent deposits (Krefft, 1867, 1870, 1871; Stirling, 1889; Hale and Tindale, 1930; Tindale, 1933; Cook, 1960, 1963; Mulvaney, 1960; Mulvaney et al., 1964; Trezise, 1970; Lampert, 1971; Thorne, 1971; Marshall, 1973; Bowdler, 1974; Ryder, 1974; M. J. Smith, 1976, 1982; Bartholomai, 1977; Hope et al., 1977; Archer and Brayshaw, 1978; Molnar, 1978, 1982; Williams, 1980; Hope, 1981; M. A. Smith, 1982; Wells et al., 1984) but is almost unknown from the Tertiary. There is one record from the Pliocene Wellington Caves (Hand et al., 1988) and one from the Miocene, based on a statement by Estes (1984) that a specimen of *Tiliqua* had been identified by J. Gauthier among the Kutjamarpu local fauna (Middle Miocene of northern South Australia; Stirton et al., 1967). Both records remain undescribed. The Kutjamarpu local fauna is considered (Archer et al., 1989) to be just older than the Dwornamor local fauna, making the former the oldest record of the *Tiliqua* lineage. The existence of this specimen in South Australia and *T. pusilla* in Queensland shows that the *Tili-*

qua lineage was widespread in Australia by the Middle Miocene.

Identification of the Riversleigh species as *Tiliqua* rather than *Cyclodomorphus* suggests that these sister taxa had diverged prior to the Middle Miocene, pushing the diversification and ultimate origin of the *Egernia* group even further back, potentially to pre-Miocene times. This scenario is incompatible with a previous hypothesis for *Egernia* of rapid Pleistocene speciation following a Pliocene origin (Horton, 1972). A preliminary dating via the 'albumin clock' of around 12 Myr BP for the *Egernia-Tiliqua* split (Baverstock and Donnellan, 1990) is thus also too recent.

The mammal fauna of the Dwornamor local fauna is dominated by arboreal browsers and has a very high diversity (Hand, 1985; Archer & Flannery, 1985; Flannery & Archer, 1987a; 1987b; Archer et al., 1988) with minimally 58 species present (Archer et al., 1989, Table 1). Such diversity would today be found only in a rainforest environment, which has supported the idea of the Dwornamor local fauna as a tropical rainforest fauna. With the exception of *T. gigas*, living species of *Tiliqua* do not inhabit rainforests, so that *T. pusilla*, combining small size and rainforest-dwelling habits, represents a radiation of the genus with no modern parallel. Possibly *Tiliqua* was a more diverse taxon in the past, and/or modern bluetongues represent a recent open-country radiation descended from dwarfish rainforest ancestors.

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